THE SOUTH AFRICAN JANOLIDAE (MOLLUSCA, NUDIBRANCHIA) WITH THE DESCRIPTION OF A NEW GENUS AND TWO NEW SPECIES

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(With 28 figures and 3 tables)

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ABSTRACT

Examination of the shallow waters of the Cape Peninsula, South Africa, has revealed the presence of three sympatric species of Janolidae. The description of *Janolus capensis* Bergh, 1907 is expanded. *Janolus longidentatus* sp. nov. is described in detail and, despite its resemblance to *J. capensis*, possesses several consistently distinct morphological characteristics. The two species differ in body shape, position of the gonopore and nephroproct, dentition of the jaws and radula, arrangement of ganglia within the central nervous system, and in several aspects of reproductive morphology. The third species differs significantly from all other members of the Janolidae in that the digestive gland surrounds the stomach rather than entering the notum and cerata. *Bonisa nakaza* gen. et sp. nov. is described in detail. The presence of intermediate morphological characters in several species of janolids necessitates the synonomy of *Janolus* Bergh, 1884, and *Antiopella* Hoyle, 1902.

CONTENTS

INTRODUCTION

The Janolidae are a family of arminacean nudibranchs consisting of 18 species in 5 genera. They are widely distributed in the temperate and tropical waters of the world. The genus *Caldukia* Burn & Miller, 1969, and the monotypic genus *Galeojanolus* Miller, 1971, are known only from Australia and New Zealand. *Proctonotus* Alder & Hancock, 1844, is also monotypic and has been reported only from Great Britain and the Brittany coast of France (Thompson & Brown 1976). *Antiopella* Hoyle, 1902, and *Janolus* Bergh, 1884, are much more widely distributed.

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Bergh (1907) described *Janolus capensis* from three specimens dredged from False Bay, south-western Cape. Intertidal and subtidal collections by means of S.C.U.B.A. around the Cape Peninsula have yielded specimens of *Janolus capensis* as well as two previously unknown species, which are here described.

Antiopella and *Janolus* have been considered as distinct genera by most workers who have studied the Janolidae (Eliot 1906; Pruvot-Fol 1954; Marcus 1958; Burn & Miller 1969; Miller 1971). The South African species possess morphological features which are intermediate between those utilized to separate *Antiopella* from *Janolus*. For this reason, a review of the generic status of the Janolidae is provided. To supplement this review, specimens of *Janolus fuscus* from California, *J. cristatus* from England, and *J. toyamensis* from Hawaii were also examined.

Janolus capensis Bergh, 1907

Figs 1A–B, 2–9

Janolus capensis Bergh, 1907: 90, pl. 7 (figs 6–21). Barnard, 1927: 207, pl. 20 (figs 6–7).

Material examined

10 specimens, 20 m depth off Llandudno (34°01′S 18°20′E), 23 December 1979

6 specimens, intertidal, Clovelly, False Bay (34°05′S 18°26′E), 17–18 January 1980

3 specimens, 10 m depth, Rooi Els (34°18′S 18°49′E), 23 January 1980

1 specimen, 10 m depth, Castle Rocks, False Bay (34°18′S 18°29′E), 12 February 1980

5 specimens, 10 m depth, Windmill Beach, False Bay (34°12′S 18°27′E), 9 October 1980

2 specimens, 10 m depth, Rooi Els (34°18′S 18°49′E), 26 October 1980

2 specimens, 5 m depth, Miller's Point, False Bay (34°14′S 18°29′E), 28 October 1980

Distribution

Atlantic and Indian Ocean coasts of the Cape Peninsula, extending eastward to Rooi Els, Cape Hangklip.

External morphology

The living animals (Fig. 1A–B) attain a length of 30 mm. The stout body is broadest anteriorly, tapering to the acute posterior end of the foot. The rhinophores (Fig. 2A) are perfoliate with 11 to 16 complete or incomplete transverse lamellae. Between the rhinophores is the large, convoluted interrhinophoral crest (caruncle) (Fig. 2B). The anus in middorsal, near the posterior limit of the notum. The head (Fig. 2C) is rounded with the mouth situated

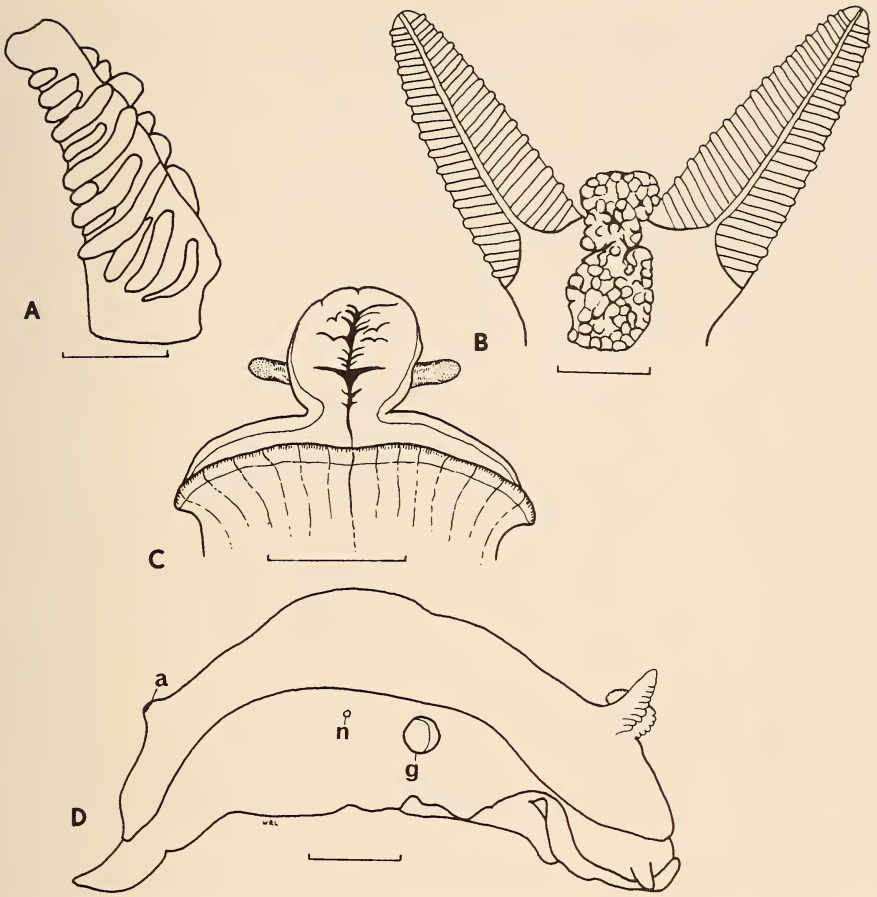

Fig. 2. *Janolus capensis* Bergh, 1907. A. Rhinophore, scale 1,0 mm. B. Inter-rhinophoral crest, scale 1,0 mm. C. Ventral view of head, scale 2,0 mm. D. Lateral view, scale 3,0 mm. Figs 2A–B, D are drawn from preserved material, Fig. 2C is from living material.

centrally. Short, blunt dorsoventrally flattened oral tentacles are present on either side of the head. The foot is rounded anteriorly with a deep transverse groove. The separate male and female gonopores are situated on the right side near the middle of the body, while the nephroproct is situated more posteriorly (Fig. 2D).

The cerata are entirely smooth, somewhat laterally compressed and are arranged in 5 to 6 closely packed longitudinal rows which are irregularly arranged. Within each ceras (Fig. 3A) are 2 to 4 irregular lobes of the digestive gland which branch near the middle of the ceras. The anteriormost cerata lack extensions of the digestive gland.

The ground colour is translucent white. Opaque white markings may be present or absent on the rhinophoral lamellae, inter-rhinophoral crest and

along the dorsolateral margin of the foot. The cerata are tipped with an apical band of opaque white guanine crystals which may have a bluish tinge. The digestive gland within the cerata varies from chocolate brown to brick red or red-orange.

Digestive system (Fig. 3B)

Near the opening of the mouth, numerous small, simple oral glands are present on the surface of the outer lips of the buccal mass. The buccal mass is large and muscular with an ovoid opening. A pair of large, highly dendritic

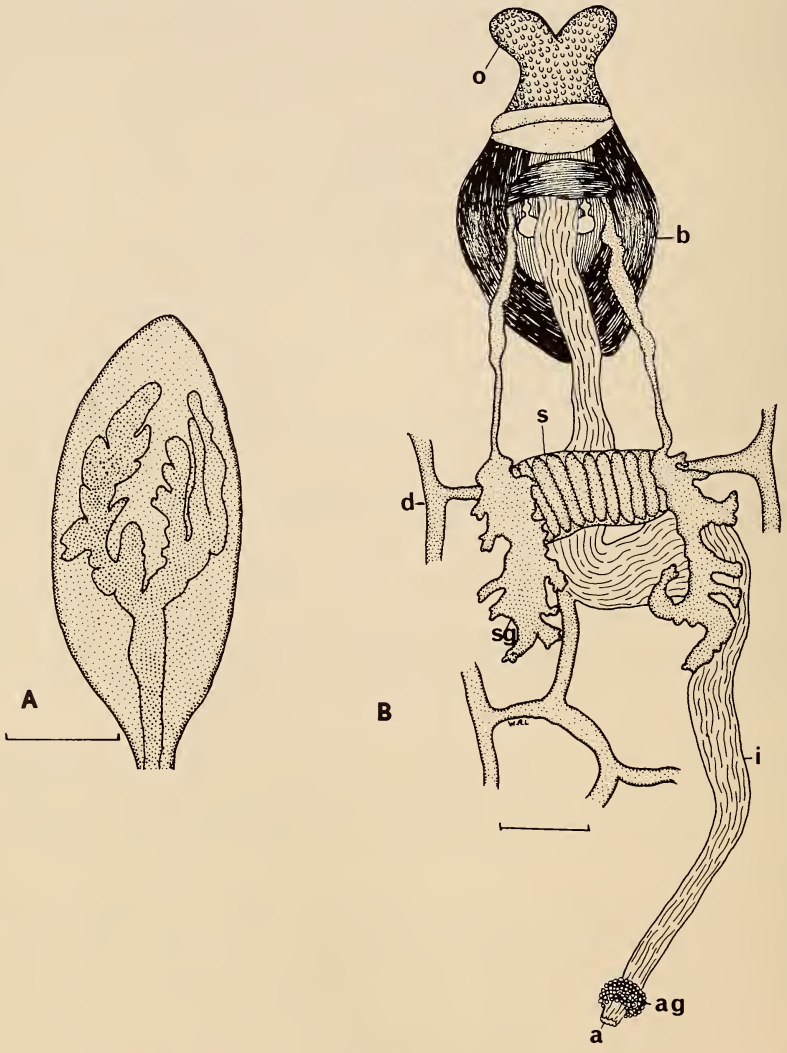

Fig. 3. *Janolus capensis* Bergh, 1907. A. Ceras dissected to show branching of digestive gland, scale 1,0 mm. B. Digestive system, scale 1,0 mm.

salivary glands extends anteriorly from the stomach and enters the buccal mass near its anterior limit via glandular ducts. The salivary glands are thick at their insertion, taper sharply and again expand into the dendritic portion. The oesophagus is wide throughout its length and enters the highly ridged stomach. Three major branches of the digestive gland emerge from the stomach. At the posterior limit of the stomach the intestine curves to the right and continues posteriorly, terminating at the medial anus. A well-developed anal gland surrounds the anus.

The buccal mass is large and muscular with an oblong opening (Fig. 4A). The paired jaws (Fig 4B) are large and strong. The inner masticatory border (Fig. 5A) is thickened and entirely smooth. There is a raised, arched portion which strengthens the masticatory edge.

The radula (Figs. 5B, 6) is broad and well developed. There may be from 17 to 21 rows of teeth with 26 to 42 lateral teeth on each side of the narrow, linear rachidian tooth. The hook-shaped lateral teeth (Fig. 6B) are smooth and sharply arched. Laterally from the centre of the radula, the lateral teeth increase in size until about one-third of the breadth of that half of the radula, at which point they again begin to diminish in size for the remaining outer two-thirds.

Central nervous system

All the major ganglia of the central nervous system (Fig. 7) are situated anteriorly in the circumoesophageal nerve ring. The cerebral and pleural ganglia are almost entirely fused, forming a pair of ganglionic masses separated by a short commissure. The anteriormost nerves on the dorsal surface of the

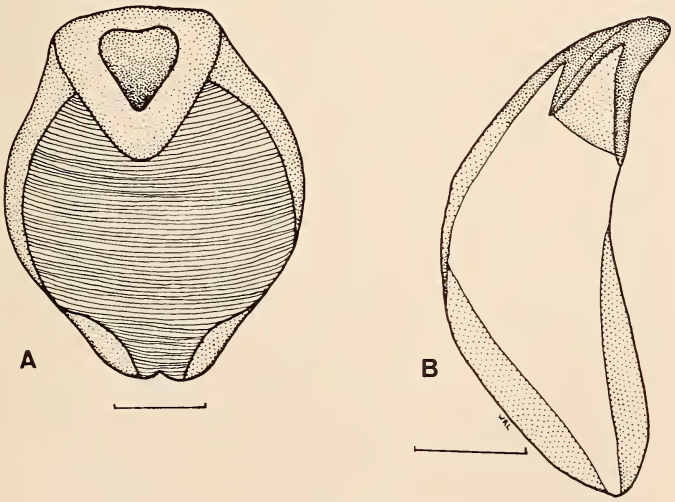

Fig. 4. *Janolus capensis* Bergh, 1907.
A. Buccal mass, scale 1,0 mm.
B. Jaw, scale 1,0 mm.

Fig. 5. *Janolus capensis* Bergh, 1907. A. Scanning electron micrograph of masticatory border of jaw, scale 300 μm between squares. B. Scanning electron micrograph of radula, scale 10 μm between squares.

Fig. 6. *Janolus capensis* Bergh, 1907. A. Scanning electron micrograph of central portion of radula. B. Scanning electron micrograph of lateral tooth from outer portion of radula. Scales 10 μm between squares.

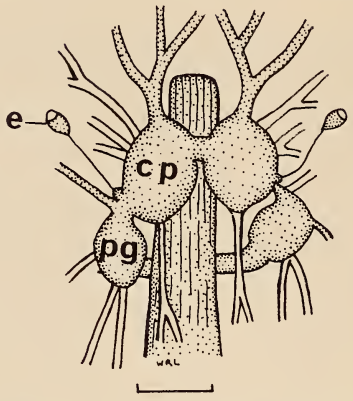

Fig. 7. *Janolus capensis* Bergh, 1907.
Central nervous system.
Scale 0,5 mm

cerebropleural ganglia bifurcate near the base. The outer branch innervates the rhinophore and a small rhinophoral ganglion is present near the apex of the nerve at the base of each rhinophore. The inner branch divides again with both branches innervating the inter-rhinophoral crest. The eyes are situated on short nerves which join the cerebropleural ganglia near their juncture with the somewhat smaller pedal ganglia. At the junction of each eye to the cerebropleural ganglia is a minute optic ganglion. Anterior to each buccal ganglion (Fig. 3B) is a minute gastro-oesophageal ganglion. The pedal ganglia are separated by a short commissure.

Reproductive system (Fig. 8)

The ovotestis consists of numerous lobes and gives rise to a slightly convoluted ampulla which subsequently narrows and bifurcates into the male

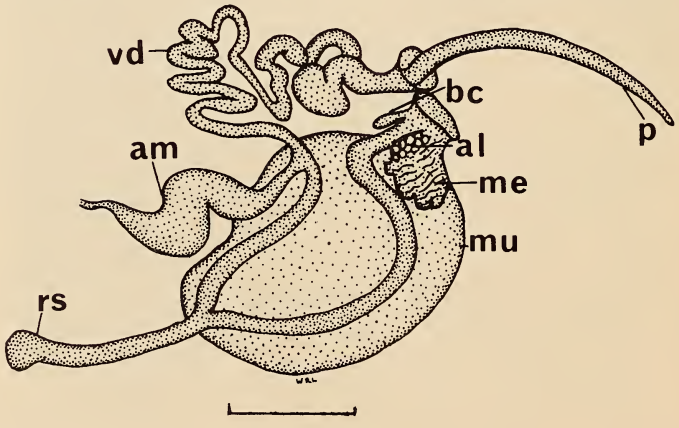

Fig. 8. *Janolus capensis* Bergh, 1907.
Reproductive system. Scale 4,0 mm.

and female ducts. The vas deferens is highly convoluted and prostatic throughout its length. It terminates at an elongate, acutely pointed penis. The extremely elongate oviduct is muscular and gives rise to a very long receptaculum seminis and continues until it joins the albumen gland of the female gland mass at the female atrium. *In situ*, the oviduct and receptaculum seminis are surrounded by the two lobes of the voluminous mucous gland. The membrane and albumen glands are significantly smaller than the mucous gland. Adjoining the oviduct and female gland mass, at the female atrium, is a small pyriform bursa copulatrix.

Egg mass

The egg mass (Fig. 9) is highly convoluted and corresponds to type B (Hurst 1967). There are 38 to 45 eggs per capsule.

Natural history

Janolus capensis is associated with, and feeds upon, several species of arborescent cheilostomatous ectoprocts, most commonly *Menipea triseriata* Busk, 1852, and *Onchoporella buskii* (Harmer, 1923). Mating individuals and egg masses are often found on ectoproct colonies as well. *Janolus capensis* is found commonly throughout the year along the Atlantic and Indian Ocean coasts of the Cape Peninsula from the intertidal to at least 40 m in depth.

Janolus longidentatus sp. nov.

Figs 1C, 10–17

Type material

Holotype—SAM–A34883, 1 specimen, 3 m depth, Miller's Point (34°14′S 18°29′E), 10 December 1980

Paratypes—SAM–A34884, 2 specimens, 10 m depth, Castle Rocks, False Bay (34°18′S 18°29′E), 1 October, 1980

SAM–A34885, 1 specimen, 5 m depth, Miller's Point, False Bay (34°14′S 18°29′E), 28 October 1980

Other material

3 specimens, intertidal, Clovelly, False Bay (34°05′S 18°26′E), 17 December 1979

2 specimens, 10 m depth, Windmill Beach, False Bay (34°12′S 18°29′E), 11 July 1980

Etymology

The epithet *longidentatus* refers to the elongate cusp of the lateral radular teeth which characterizes this species.

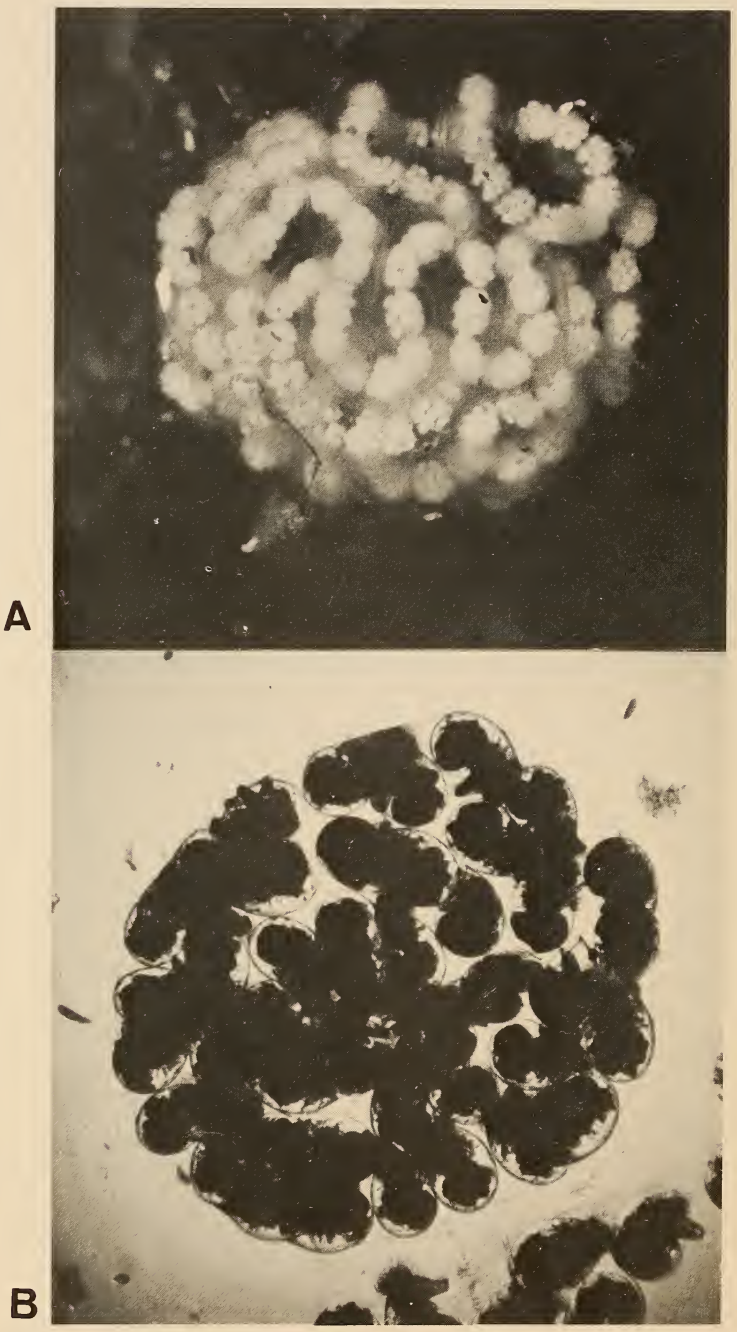

Fig. 9. *Janolus capensis* Bergh, 1907.
A. Egg mass × 6.
B. Single egg capsule × 50.

External morphology

Fully mature specimens (Fig. 1C) attain a maximum length of 20 mm. The slender body is widest anteriorly, tapering to an acute posterior margin of the foot. The rhinophores (Fig. 10A) are perfoliate with 9 to 12 complete or incomplete, transverse lamellae. The inter-rhinophoral crest (Fig. 10B) is highly convoluted, narrowest in the middle. The anus is situated mid-dorsally near the posterior end of the notum. The mouth is located centrally on the ventral side of the rounded head (Fig. 10C). A pair of short, blunt oral tentacles extend from either side of the head. The anteriorly rounded foot possesses a deep transverse groove at its anterior limit. The separate male and female gonopores are situated laterally in the anterior third of the right side of the body, while the nephroproct is located more posteriorly, but within the anterior half of the body (Fig. 10D).

The entirely smooth cerata are long and slender, arranged in 4 or 5 irregular, longitudinal rows. Within each ceras there are 2 main branches of the digestive gland which usually branch again above the base of the ceras (Fig. 11). The anteriormost cerata lack extensions of the digestive gland within them.

The general body colour of living animals is translucent white, with a pink or blue cast. Varying amounts of opaque white pigment are present on the rhinophores and at the apices of the cerata. The digestive gland within the cerata is chocolate brown to red-orange.

Digestive system

Near the mouth and surrounding the outer lips of the buccal mass is a narrow ring of small, simple oral glands. The buccal mass (Fig. 12A) is somewhat dorsoventrally compressed, muscular, with a circular opening. The paired salivary glands are very thin anteriorly and expand posteriorly into the dendritic, glandular portion with numerous ramifications. The oesophagus is a straight glandular tube which expands into the corrugated, saccate stomach. From the stomach arise three major branches of the digestive gland: two branches emanate from the anterodorsal portion of the stomach and give rise to the left and right anterior digestive branches; the third branch arises at the ventral portion of the stomach and branches to the right and left posterior digestive branches. The intestine emerges from the posterior portion of the stomach and curves to the right, continuing posteriorly to the anus. The anus is surrounded by a large anal gland.

The jaws (Figs 12B, 13A) are of moderate thickness, angular and terminate posteriorly in a rather acute point. The masticatory border consists of 7 or 8 large, rounded denticles. The radula (Figs 13B, 14) is broad, consisting of 18 to 23 rows of teeth. There are 19 to 26 gradually arched, edenticulate lateral teeth on each side of the somewhat broad rachidian tooth. In the ten specimens examined, the rachidian teeth all possess 6 to 10 minute striations on each side of the base of the elongate central cusp. The lateral teeth have an elongate cusp

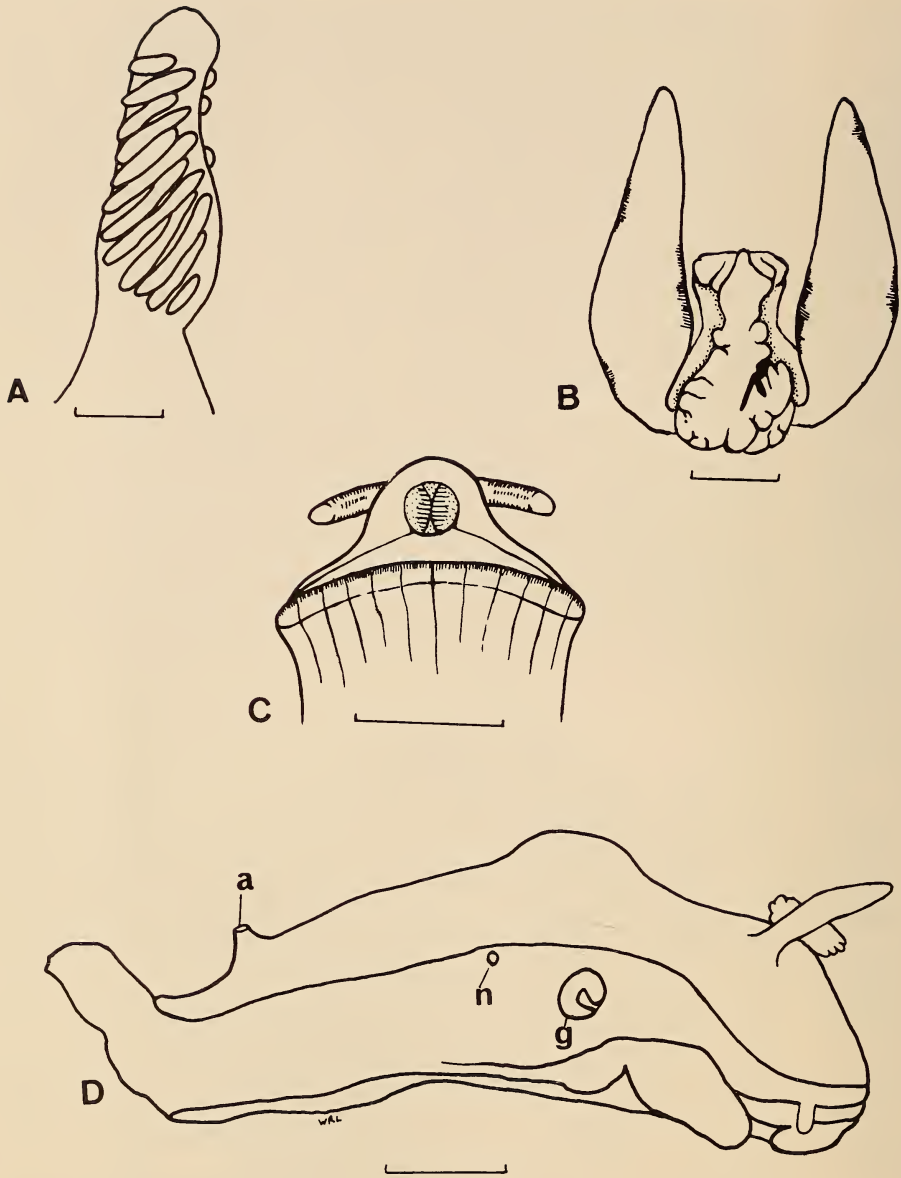

Fig. 10. *Janolus longidentatus* sp. nov. A. Rhinophore, scale 0,5 mm. B. Inter-rhinophoral crest, scale 0,5 mm. C. Ventral view of head, scale 1,5 mm. D. Lateral view, scale 2,0 mm. Figs 2A–B, D are drawn from preserved material, Fig. 2C is from living material.

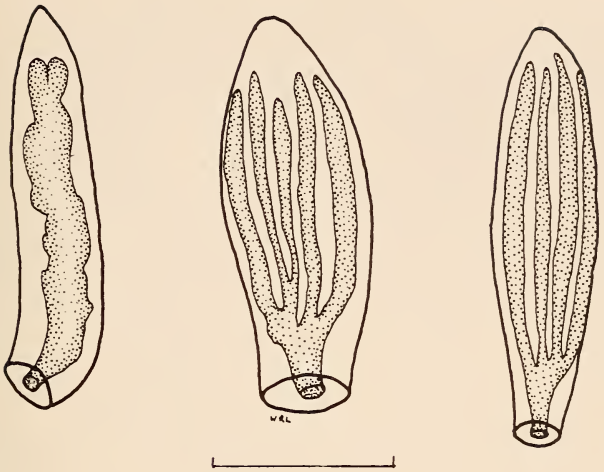

Fig. 11. *Janolus longidentatus* sp. nov.
Cerata dissected to show branching of digestive gland.
Scale 1,0 mm.

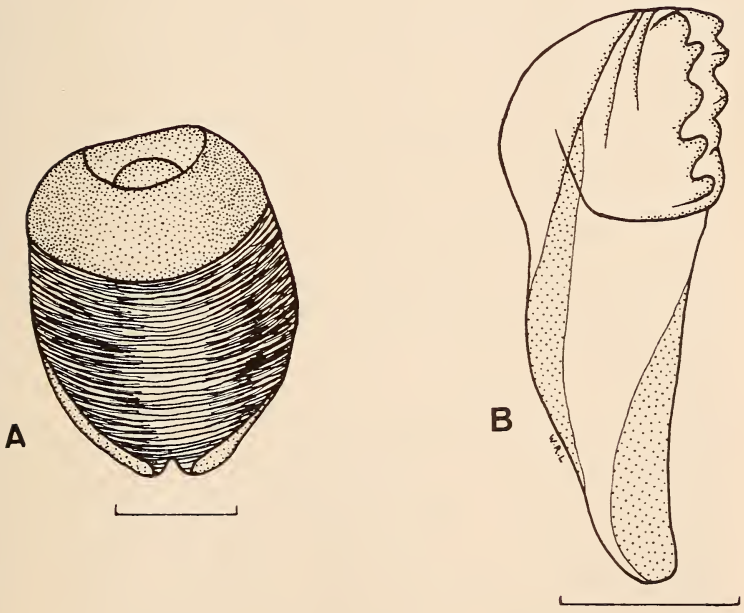

Fig. 12. *Janolus longidentatus* sp. nov.
A. Buccal mass, scale 1,0 mm.
B. Jaw, scale 1,0 mm.

Fig. 13. *Janolus longidentatus* sp. nov. A. Scanning electron micrograph of masticatory border of jaw, scale 300 μm between squares. B. Scanning electron micrograph of radula, scale 10 μm between squares.

Fig. 14. *Janolus longidentatus* sp. nov. A. Scanning electron micrograph of central portion of radula, scale 30 μm. B. Scanning electron micrograph of lateral teeth from outer portion of radula, scale 30 μm between squares.

and increase in length towards the outer edges of the radula. Only the outermost teeth decrease in length.

Central nervous system (Fig. 15)

The major ganglia are situated in the circumoesophageal nerve ring. The cerebral and pleural ganglia are largely distinct. The anteriormost nerve of the dorsal surface of the cerebral ganglia bifurcates near its base with the inner branch innervating the inter-rhinophoral crest and the outer branch innervating the rhinophores. There is a distinct rhinophoral ganglion near the apex of the rhinophoral nerve. The eyes are situated at the apex of short optic nerves which join the central nervous system via small optic ganglia at the junction of the cerebral and pleural ganglia. Extending from the cerebral ganglia are the buccal nerves which join the round buccal ganglia. Anterior to each buccal ganglion is a minute gastro-oesophageal ganglion. The pedal ganglia are long with an elongate commissure between them.

Reproductive system (Fig. 16)

The follicles of the ovotestis are numerous and arranged into distinct lobes. The thick ampulla has 2 or 3 convolutions and narrows to the bifurcation of the vas deferens and oviduct. The glandular prostatic vas deferens is short with few convolutions. It enlarges into a much thicker penis sac which is recurved to an acutely pointed unarmed penial papilla. The muscular oviduct is embedded

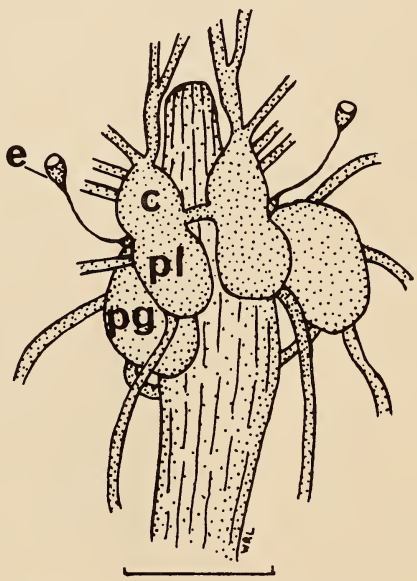

Fig. 15. *Janolus longidentatus* sp. nov.
Central nervous system.
Scale 1,0 mm.

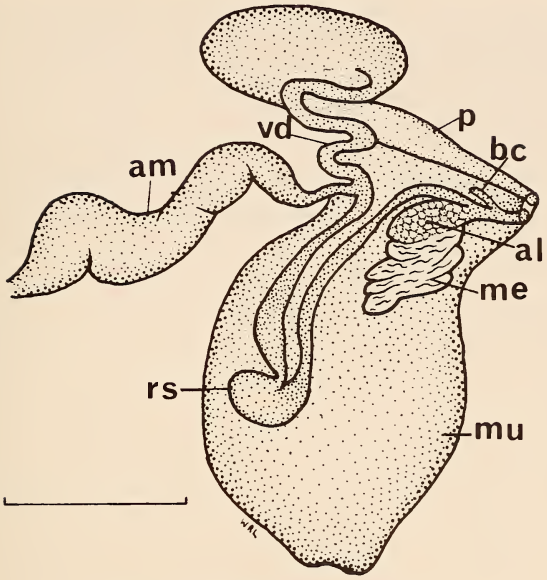

Fig. 16. *Janolus longidentatus* sp. nov.
Reproductive system.
Scale 1,0 mm.

between two lobes of the mucous gland and branches near the middle of its length to a short, bulbous receptaculum seminis. The major branch continues distally to its connection with the albumen gland and female gonopore. The narrow, linear bursa copulatrix joins the oviduct near the junction of the female gland mass, at the female atrium.

Egg mass (Fig. 17)

The egg mass is a low, flat spiral consisting of 3 or 4 whorls and corresponds to type B (Hurst 1967). There are 5 to 9 eggs per capsule.

Natural history

Janolus longidentatus feeds upon the cheilostomatous ectoproct *Menipea triseriata* Busk. It is commonly found in False Bay but has not been encountered on the Atlantic coast of the Cape Peninsula. *J. longidentatus* appears to have a seasonal distribution. Specimens have not been found from February to July and appear to be present largely in the winter and spring months. Specimens have been found from the intertidal to 30 m depth.

Bonisa gen. nov.

Diagnosis

Body stout, ovoid in outline. Rhinophores perfoliate. Inter-rhinophoral crest low, triangular with few convolutions. Cerata smooth, caducous, not

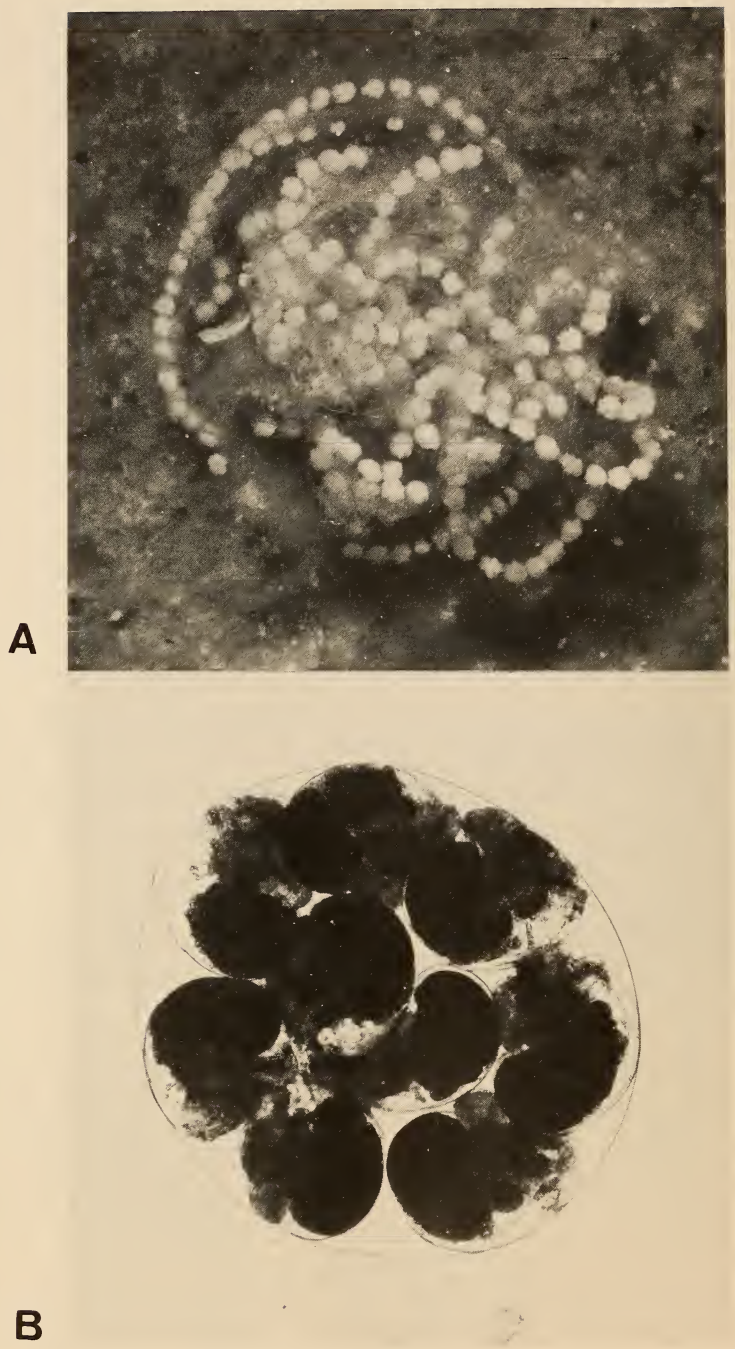

Fig. 17. *Janolus longidentatus* sp. nov.
A. Egg mass × 6.
B. Single egg capsule × 100.

containing branches of digestive gland. Gonopore near middle of body with nephroproct in posterior third of body. Oral glands small, simple. Salivary glands well developed with basal bulb. Digestive gland of three lobes surrounding stomach, not extending into notum or cerata. Anal glands absent. Jaws thick with smooth masticatory border. Rachidian and lateral teeth weakly to strongly denticulate. Pedal ganglia lateral to well separated cerebral and pleural ganglia. Optic nerves elongate. Reproductive system hermaphroditic, androdiaulic. Vas deferens short, prostatic, expanding into blunt, corrugated penis. Receptaculum seminis large, muscular and adjacent to gonopore. Bursa copulatrix small, linear and joining receptaculum seminis at female gonopore.

Type species

Bonisa nakaza sp. nov.

Etymology

Bonisa is named for my wife Bonnie Isabel Julien Gosliner.

Bonisa nakaza sp. nov.

Figs 1D–F, 18–25

Type material

Holotype—SAM–A34886, 20 m depth, off Llandudno (34°01′S 18°20′E), 23 December 1979.

Paratypes—SAM–A34887, 4 whole specimens, 20 m depth, off Llandudno (34°01′S 18°20′E), 23 December 1979

Other material

1 specimen, 10 m depth, Oudekraal (33°59′S 18°21′E), 13 January 1980

2 specimens, 10 m depth, Castle Rocks, False Bay (34°18′S 18°29′E), 17 January 1980

Etymology

Nakaza is a Zulu word meaning 'to adorn with beautiful colours', and the name is based on the bright coloration typical of this species.

External morphology

Fully mature specimens may reach a length of 100 mm. The body is broad, roughly oval in outline. The rhinophores (Fig. 18A) are perfoliate with 14 to 23 transverse lamellae. The slightly convoluted inter-rhinophoral crest (Fig. 18B) is triangular in shape, widest anteriorly. The mid-dorsal anus is located near the posterior end of the notum. The broad head (Fig. 18C) is round in shape, with a secondary, anterior lobe. The paired oral tentacles are moderately elongate and situated on either side of the head. The foot is transversely grooved at its

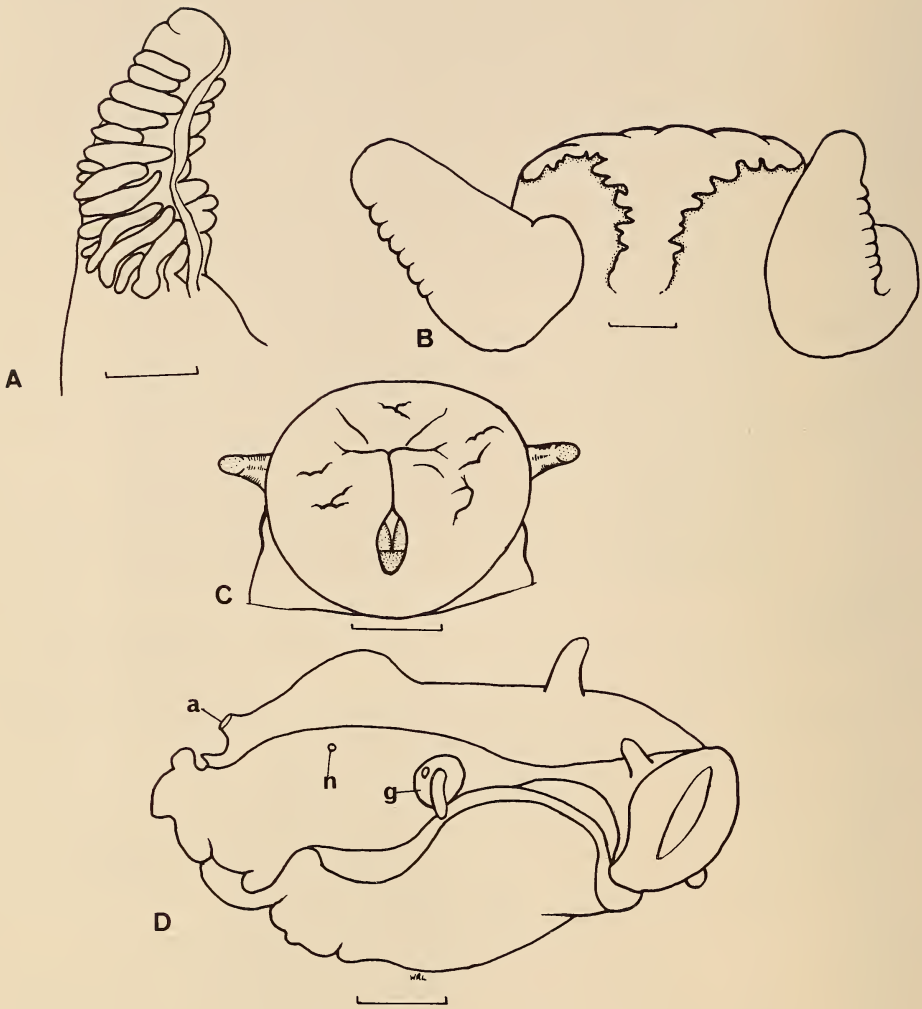

Fig. 18. *Bonisa nakaza* gen. et. sp. nov. A. Rhinophore, scale 1,0 mm. B. Inter-rhinophoral crest, scale 1,0 mm. C. Ventral view of head, scale 1,0 mm. D. Lateral view, scale 5,0 mm. Figs 2A–B, D are drawn from preserved material, Fig. 2C is from living material.

anterior limit. The separate male and female gonopores are located near the middle of the right side of the body (Fig. 18D). The nephroproct is situated more posteriorly, in the posterior third of the animal. The elongate, readily caducous cerata are smooth and cylindrical. They are arranged in 16 to 21 diagonal rows per side with 8 to 10 cerata per row. Within the cerata a central muscular duct is present but this contains no extension of the digestive gland. At the base of each ceras is a ganglion which bifurcates into two nerves which extend distally into the ceras (Fig. 19A).

The living animals are variably and brightly coloured. (Fig. 1D–F). The general body colour ranges from translucent white to yellow or yellow-orange. Yellow or orange pigment is particularly concentrated on the anterodorsal surface. The rhinophores possess varying amounts of yellow or orange pigment. The cerata are strikingly variable in their coloration. On the surface they are most commonly yellow, basally, with varying amounts and shades of blue pigment on the more distal portion. Some specimens possess a small subapical concentration of black or dark-blue pigment within the ceratal ducts. Other

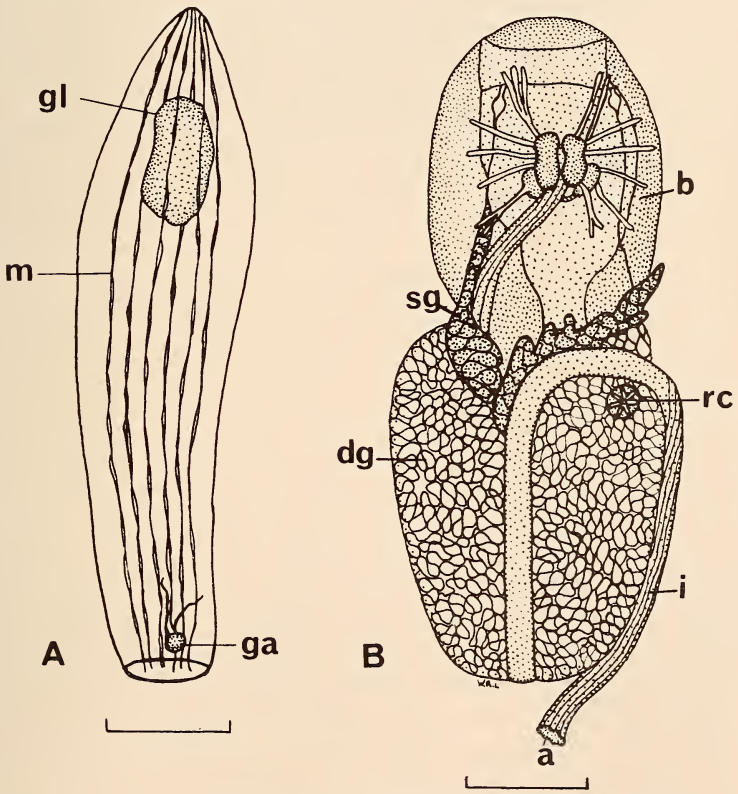

Fig. 19. *Bonisa nakaza* gen. et sp. nov.
A. Ceras, scale 1,0 mm.
B. Digestive system, scale 2,0 mm.

specimens, which entirely lack blue or yellow pigment, possess only an apical band of orange on each ceras and rhinophore. A few juvenile specimens have cerata which are pinkish with blue pigment and opaque white apices. Since adult specimens of different colour patterns have been observed copulating, they are considered to be conspecific.

Digestive system (Fig. 19B)

There is a moderately large ring of oral glands surrounding the outer lips. The massive buccal mass is highly muscular and occupies the anterior third of the body cavity. The paired salivary glands are well developed, extending from the posterior limit of the oesophagus. Near their origin there is a large, spherical expansion of the salivary gland duct which probably functions as a vestibule for storage of secretory products. The oesophagus is short and expands into a thin-walled stomach. On the dorsal surface of the stomach is a large corrugated portion. Surrounding the stomach are three major lobes of the highly dendritic digestive gland. A digestive lobe joins the stomach on both the anterolateral sides of the stomach with a third lobe connecting to the anteroventral portion. The intestine emerges from the posteroventral portion of the stomach and continues posteriorly to the anus. The anus is not surrounded by anal glands.

The buccal mass (Fig. 20A) has an oblong opening. The jaws (Fig. 20B) are thick and broad with a smooth masticatory border (Fig. 21) which is supported by an elevated arch of chitin. The outer borders of the jaws are sharply indented. The radula (Fig. 22) contains 21 to 46 rows of teeth with 7 to

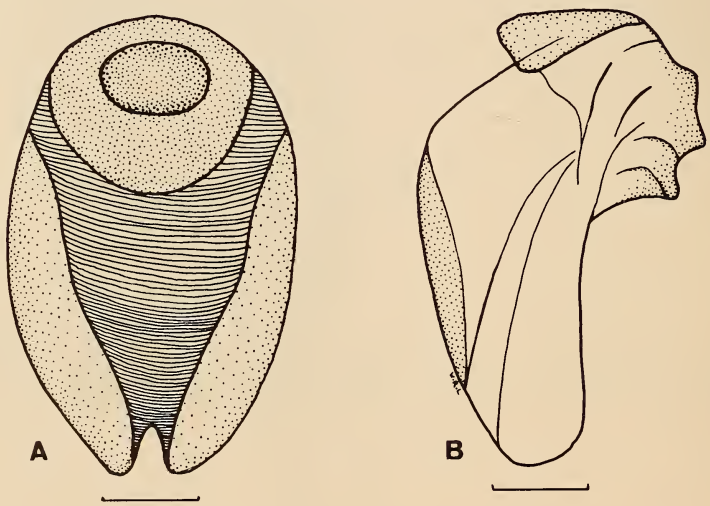

Fig. 20. *Bonisa nakaza* gen. et sp. nov.
A. Buccal mass, scale 1,0 mm.
B. Jaw, scale 1,0 mm.

Fig. 21. *Bonisa nakaza* gen. et sp. nov. Scanning electron micrograph of masticatory border of jaw. Scale 100 μm between squares.

33 laterals on each side of the rachidian teeth. The rachidians possess 2 to 5 small or elongate denticles. The lateral teeth possess 2 to 7 denticles on each side of the elongate central cusp.

Central nervous system (Fig. 23)

The major ganglia of the central nervous system are situated in the circumoesophageal nerve ring. The cerebral ganglia are closely appressed to each other without a distinct commissure and are joined posteriorly by the distinct pleural ganglia. The anteriormost dorsal nerve of the cerebral ganglion innervates the rhinophores and divides near the middle of its length to give rise to a very thin branch which innervates the inter-rhinophoral crest. The eyes are situated at the distal end of the elongate optic nerve which joins the junction of the cerebral and pleural ganglia via a short optic ganglion. Extending anteriorly from the cerebral ganglia are the paired buccal nerves which enlarge into the buccal ganglia on the surface of the buccal mass. Ventral to the oesophagus, the buccal ganglia are joined by a commissure of moderate length and anteriorly each gives rise to a small gastro-intestinal ganglion. The pedal ganglia are situated laterally to the cerebral and pleural ganglia rather than posteriorly, and are connected by an elongate commissure.

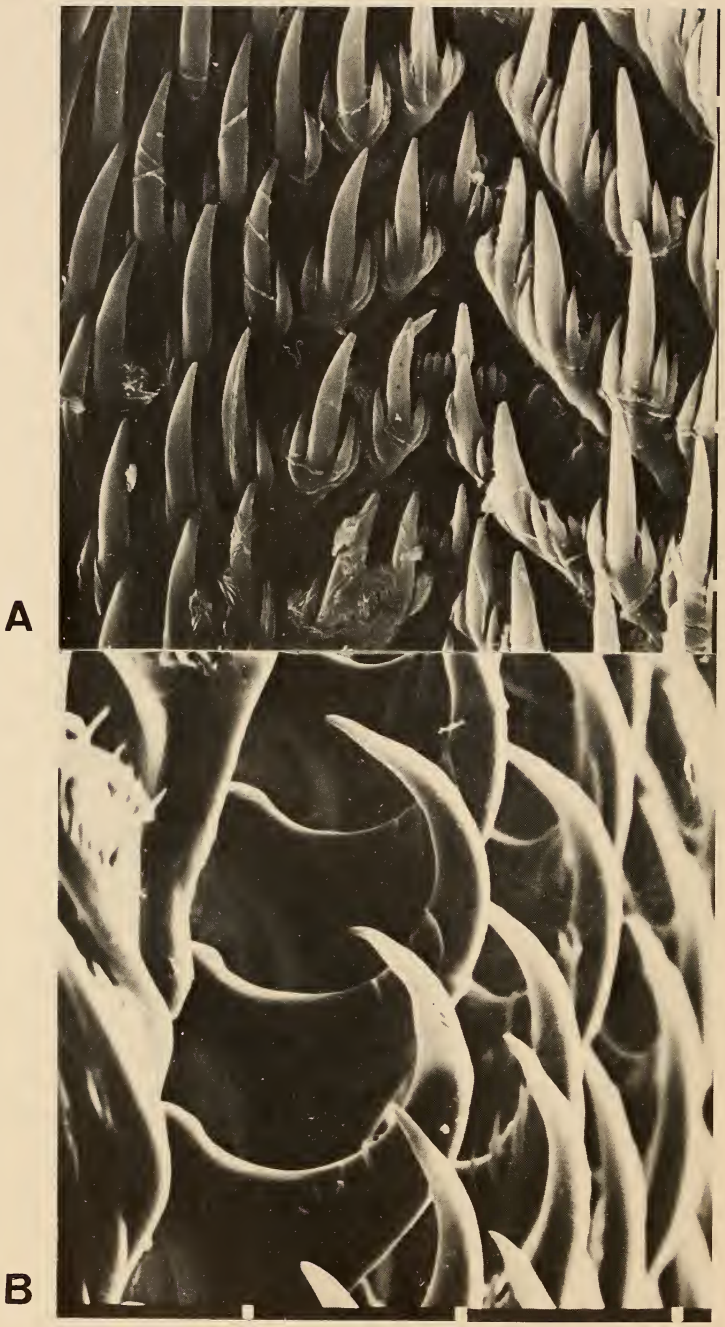

Fig. 22. *Bonisa nakaza* gen. et sp. nov. A. Scanning electron micrograph of central portion of radula. B. Scanning electron micrograph of lateral teeth from outer portion of radula. Scales 30 μm between squares.

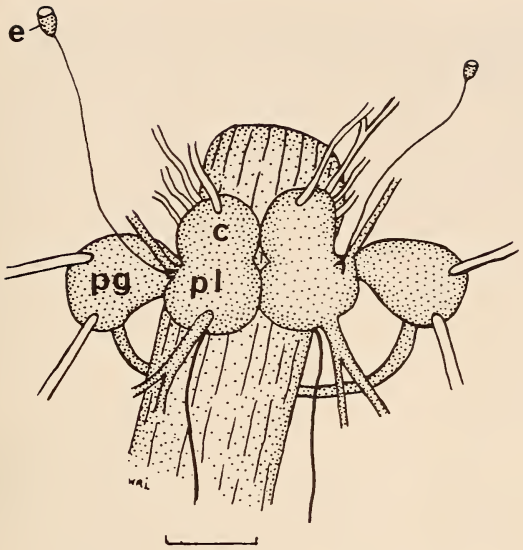

Fig. 23. *Bonisa nakaza* gen. et sp. nov.
Central nervous system.
Scale 0,5 mm.

Reproductive system (Fig. 24)

The ovotestis consists of numerous follicles which are united into an ovoid mass. The preampullary duct emerges from the anterior end of the ovotestis and expands into a highly convoluted, thickened ampulla. The ampulla narrows anteriorly and divides into the oviduct and vas deferens. The vas deferens is short, thick, and muscular, and expands into the massive penis sac. The penial papilla is club-shaped and strongly corrugated. The oviduct is muscular and joins the large receptaculum seminis near its base. Traversing the base of the receptaculum seminis is a small, linear bursa copulatrix which joins the receptaculum near the female gonopore. At the base of the receptaculum sac is a thick duct which connects it with the small albumen and membrane portions of the female gland mass. These glands join the massive mucous gland, which forms the bulk of the female gland mass.

Egg mass (Fig. 25)

The egg mass is about 20 to 30 mm high, consists of numerous convolutions and corresponds to type B (Hurst 1967). There are one or two eggs per capsule. The egg mass is frequently deposited on the finger-like projections of gorgonians.

Natural history

Bonisa nakaza is found in the shallow subtidal, at depths of 3 to 30 m on both the Atlantic and Indian Ocean coasts of the Cape Peninsula. It is

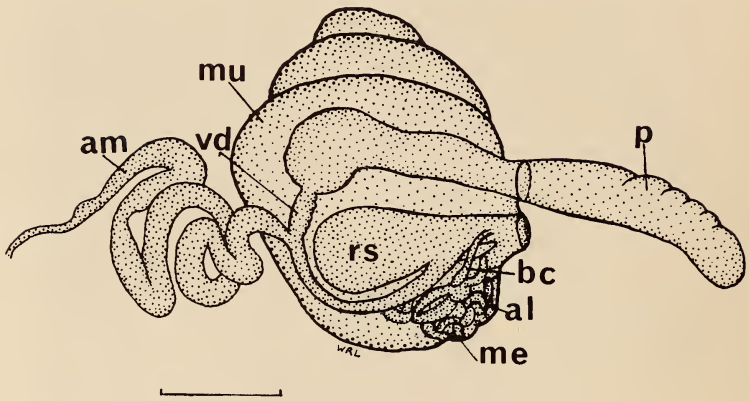

Fig. 24. *Bonisa nakaza* gen. et sp. nov.
Reproductive system.
Scale 4,0 mm.

associated with and feeds upon the heavily calcified arborescent cheilostomatous ectoproct, *Tubucellaria levinseni* Canu & Bassler, 1930.

DISCUSSION OF THE JANOLIDAE

Within the suborder Arminacea, the tribe Pachygnatha is subdivided into three families, the Madrellidae, Dironidae, and Janolidae (Franc 1968). The Janolidae have been separated from the other two families by having a broad rather than narrow radula, a medial rather than lateral anus, and by having extensions of the digestive gland into the cerata. With the discovery of *Bonisa nakaza* in this study, the diagnosis of the Janolidae must be expanded to include forms with or without extensions of the digestive gland into the cerata.

The family Janolidae has been previously subdivided into five genera. *Proctonotus* Alder & Hancock, 1844, and *Caldukia* Burn & Miller, 1969, lack an inter-rhinophoral crest. *Caldukia* can be separated from *Proctonotus* by its distinctively stout rhinophores with transverse lamellae and its significantly narrower radular ribbon. Of the genera which possess an inter-rhinophoral crest *Galeojanolus* Miller, 1971, can be separated from *Janolus* Bergh, 1884, and *Antiopella* Hoyle, 1902, by the helmet-like appendage extending anteriorly from the head. *Bonisa* gen. nov. must be added to this group and can be readily separated from the other janolids by the fact that the digestive gland surrounds the stomach rather than entering the notum and cerata. In several respects *Bonisa nakaza* most closely approaches *Galeojanolus ionnae* Miller, 1971. Both species have an ovoid body shape, similar coloration, perfoliate rhinophores, a low, broad inter-rhinophoral crest with few convolutions, jaws with a smooth masticatory border, a moderately broad radula with strongly denticulate teeth and a diaulic reproductive system. Both species lack anal glands. However, there are several significant differences which distinguish the species. *Galeo-*

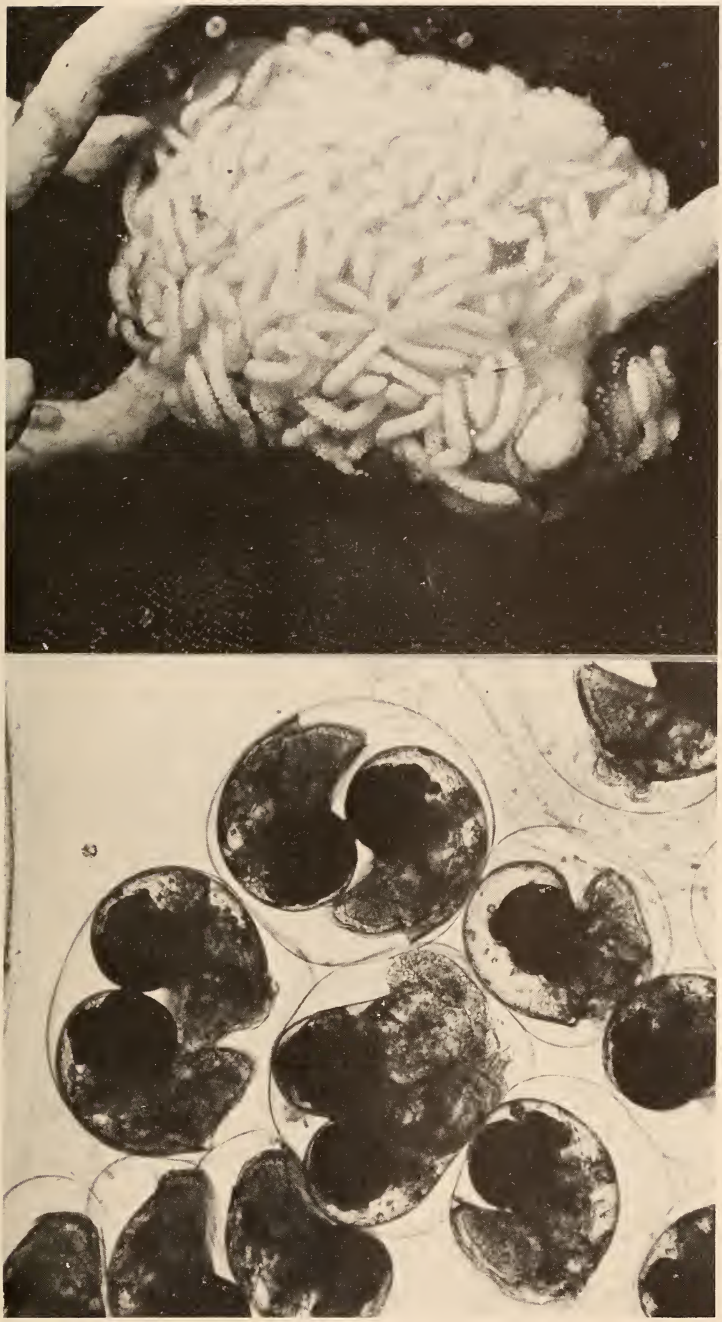

Fig. 25. *Bonisa nakaza* gen. et sp. nov.
A. Egg mass × 3.
B. Several egg capsules × 100.

janolus ionnae possesses an elongate helmet-like appendage on the anterior end of the head which may be used in capturing mobile prey (Miller 1971), while there is a short lobe anterior to the head of *Bonisa nakaza*. *G. ionnae* has papillate, inflated cerata, while they are smooth and cylindrical in *B. nakaza*. *B. nakaza* lacks complex oral glands and is devoid of digestive gland ducts in the cerata which are both present in *G. ionnae*. The reproductive system of *G. ionnae*, while not fully mature, has a conical, tapered penis and an elongate vas deferens, while *B. nakaza* has a short vas deferens and a blunt, corrugated penis similar in shape to that described for *Janolus cristatus* (Schmekel 1970). Miller described a bursa copulatrix in *G. ionnae*, while *B. nakaza* possesses both a large receptaculum seminis and a small bursa copulatrix situated near the gonopore. These differences, particularly those of the digestive system, warrant generic as well as specific separation.

It is difficult to separate *Antiopella* and *Janolus*. Several authors have united the genera (Thiele 1931; Franc 1968; Thompson & Brown 1976), while others have maintained them as distinct (Eliot 1906; Pruvot-Fol 1954; Marcus 1958; Burn & Miller 1969; Baba & Abe 1970; Miller 1971). Pruvot-Fol (1954) stated that *Antiopella* may be separated from *Janolus* by virtue of the fact that the component species possess a denticulate instead of smooth masticatory border of the jaw, smooth instead of papillate cerata, and branched instead of undivided ducts of the digestive gland within the cerata. However, several species of janolids (Table 1) possess intermediate or variable character states or individual characters. They may also possess a mixture of '*Antiopella*' and '*Janolus*' characters. Marcus (1958: 40) noted that the structure of the cerata in the type species of *Janolus*, *J. australis*, is questionable. Several workers who have suggested the separation of *Antiopella* from *Janolus* have stated that jaw denticulation alone should not warrant generic separation (Pruvot-Fol 1954; Marcus 1958). The fact that *Janolus capensis* and *J. longidentatus* are very similar in many aspects of their external and internal anatomy (present study) but differ in jaw denticulation supports the view that this character alone should not be utilized for generic separation in the Janolidae. The division of the genital ducts into a diaulic or triaulic configuration varies significantly within *Janolus* and *Antiopella*. The reproductive anatomy is described for eight of the fifteen species described in both genera. In three species, *A. mucloc* (Marcus 1958), *Janolus comis* (Marcus 1958), and *J. toyamensis* (present

TABLE 1

Antiopella and *Janolus* characteristics in three species of janolids.

Species	Ceratal epithelium	Ceratal ducts	Jaws
Janolus toyamensis	smooth or with few tubercles (A or I)	branched (A)	large denticles (I)
Janolus capensis	smooth (A)	branched (A)	smooth (J)
Janolus fuscus	smooth (A)	branched (J)	denticulate (A)

A—*Antiopella* I—Intermediate J—*Janolus*

study), the reproductive system is triaulic. In *A. cristata* (Schmekel 1970), *J. hyalinus* (Schmekel 1970), *J. fuscus* (present study), *J. capensis* (present study), and *J. longidentatus* (present study) a diaulic configuration is present. The reproductive system of the type species of *Janolus*, *J. australis*, is incompletely described. There is no correlation between division of the genital ducts and jaw denticulation. There is, therefore, little basis for separating *Antiopella* Hoyle, 1902, from *Janolus* Bergh, 1884, and *Antiopella* is here regarded as a junior subjective synonym of *Janolus* on the basis of priority.

KEY TO THE GENERA OF THE JANOLIDAE

1	Digestive gland surrounding stomach	*Bonisa*
	Digestive gland extending into notum and cerata	2
2	Inter-rhinophoral crest present	3
	Inter-rhinophoral crest absent	4
3	Head with helmet-like extension	*Galeojanolus*
	Head without extension	*Janolus*
4	Rhinophoral club stout with transverse lamellae, radula 6.1.6	*Caldukia*
	Rhinophores with inconspicuous lamellae, radula broad	*Proctonotus*

The following species are considered to constitute the family Janolidae (*indicates type species):

Bonisa **gen. nov.**

1. **Bonisa nakaza* **sp. nov.**

Caldukia Burn & Miller, 1969

2. **Caldukia affinis* (Burn, 1958)

Proctonotus? affinis Burn, 1958: 32, fig. 8, pl. 7 (fig. 15).
Caldukia affinis (Burn, 1958), Burn and Miller, 1969: 23, figs 1–2, pl. 2.

3. *Caldukia albolineata* Miller, 1970

Caldukia albolineata Miller, 1970: 279, figs 1–10.

4. *Caldukia rubiginosa* Miller, 1970

Caldukia rubiginosa Miller, 1970: figs 11–21.

Galeojanolus Miller, 1971

5. **Galeojanolus ionnae* Miller, 1971

Galeojanolus ionnae Miller, 1971: 491, figs 1–4.

Janolus Bergh, 1884

6. **Janolus australis* Bergh, 1884

Janolus australis Bergh, 1884: 19, pl. 8 (figs 15–22), pl. 9 (figs 6–8).

7. *Janolus barbarensis* (Cooper, 1863)

Aeolis barbarensis Cooper, 1863: 59.
Janolus coeruleopictus Cockerell & Eliot, 1905: 48, pl. 8 (figs 12–16). O'Donoghue, 1922: 141.
Janolus barbarensis (Cooper, 1863), O'Donoghue, 1922: 141.
Antiopella aureocincta MacFarland, 1966: 303, pl. 57 (figs 1–5), pl. 63 (figs 13–30), pl. 64 (figs 11–17). Roller, 1970: 372, in part.

8. *Janolus capensis* Bergh, 1907

Janolus capensis Bergh, 1907: 90, pl. 7 (figs 6–21).

9. *Janolus comis* Marcus, 1955

Janolus comis Marcus, 1955: 170, pl. 25 (figs 226–236).

10. *Janolus cristatus* (Chiaje, 1841)

Eolis cristatus Chiaje, 1841: pl. 88 (figs 1–12).
Janus spinolae Verany, 1845: 24, pl. 2 (fig. 9). Pruvot-Fol, 1954: 375.
Antiopa splendida Alder & Hancock, 1848: 190. Alder & Hancock, 1851.
Antiopella cristata (Chiaje, 1841), Hoyle, 1902: 214.
Janolus cristatus (Chiaje, 1841), O'Donoghue, 1924: 1.

11. *Janolus flagellatus* Eliot, 1906

Janolus flagellatus Eliot, 1906: 374.

(Likely a junior synonym of *J. hyalinus* (Alder & Hancock, 1854). Eliot (1910) considered this as an uncertain species. It was distinguished from *J. hyalinus* by possession of a flagellar penis which has subsequently been described in *J. hyalinus* (Schmekel 1970).)

12. *Janolus fuscus* O'Donoghue, 1924

Janolus fuscus O'Donoghue, 1924: 16, pl. 2 (figs 18–20).
Antiopella aureocincta Johnson & Snook, 1927: 500. Nomen nudum, Steinberg, 1963: 66.
Antiopella aureotincta MacGinitie & MacGinitie, 1949: 135. Nomen nudum, Steinberg, 1963: 66.
Antiopella aureocincta MacFarland, 1966: 303, pl. 57 (figs 1–5), pl. 63 (figs 13–30), pl. 64 (figs 11–17). Roller, 1970: 372, in part.

13. *Janolus hyalinus* (Alder & Hancock, 1854)

Antiopa hyalina Alder & Hancock, 1854*a*: 105.
Janolus hyalinus (Alder & Hancock, 1854), Eliot, 1906: 374.

14. *Janolus indicus* (Eliot, 1909)

Antiopella indica Eliot, 1909: 143.
Janolus indicus (Eliot, 1909), **comb. nov.**

15. *Janolus longidentatus* **sp. nov.**

16. *Janolus mirabilis* Baba & Abe, 1970

Janolus mirabilis Baba & Abe, 1970: 65, figs 2–3.

17. *Janolus mucloc* (Marcus, 1958)

Antiopella mucloc Marcus, 1958: 37, figs 62–71.
Janolus mucloc (Marcus, 1958), **comb. nov.**

18. *Janolus novozealandicus* (Eliot, 1907)

Antiopella novozealandica Eliot, 1907: 331.
Janolus novozealandicus (Eliot, 1907), **comb. nov.**

19. *Janolus praeclarus* (Bouchet, 1975)

Antiopella praeclara Bouchet, 1975: 127, pl. 1 (fig. 3), fig. 5.
Janolus praeclarus (Bouchet, 1975), **comb. nov.**

20. *Janolus toyamensis* Baba & Abe, 1970

Janolus toyamensis Baba & Abe, 1970: 63, fig. 1.

Proctonotus Alder & Hancock, 1844

21. **Proctonotus mucroniferus* (Alder & Hancock, 1844)

Venilia mucronifera Alder & Hancock, 1844: 163, pl. 2.
Proctonotus mucroniferus (Alder & Hancock, 1844) Alder, 1844: 407.
Zephyrina pilosa Quatrefages, 1844: 130, pl. 3 (fig. 1), pl. 4 (fig. 1), pl. 5 (figs 1–2), pl. 6 (figs 1, 11–12). Pruvot-Fol, 1954: 372.

Morphological variability

Janolus varies in its external and internal morphology. The major morphological features and their character states in the fifteen described species of *Janolus* are summarized in Table 2. Many taxa are incompletely described, including the type species, but the available morphological data does permit a review of the variability within the genus. All described species have a simply rounded head, perfoliate or, exceptionally, papillate (*J. comis* Marcus, 1955) rhinophores, an inter-rhinophoral crest, and cerata which contain ducts of the digestive gland. The inter-rhinophoral crest may be small and rectangular or may be highly elaborate as in *J. cristatus* (Alder & Hancock 1854*b*), *J. capensis* (present study), *J. novozealandicus* (Eliot 1907), and *J. longidentatus* (present study). The cerata are papillate in *J. comis* (Marcus 1955), *J. hyalinus* (Alder & Hancock 1854*b*), and *J. mirabilis* (Baba & Abe 1970), and smooth in the remainder of the species. The cerata of *J. toyamensis* are variable, with scattered, small papillae (Baba & Abe 1970) or with an entirely smooth surface (present study). The digestive gland may extend only within the basal half of the cerata in *Janolus comis* (Marcus 1958), *J. hyalinus* (Bergh 1904), and *Galeojanolus ionnae* (Miller 1971), or extend to the apex of the cerata in the remaining species of *Janolus*. Within the cerata the digestive gland may be branched or unbranched. In species with a branched digestive gland, the splitting may occur apically in *J. cristatus* (Alder & Hancock 1854*b*) and *J. barbarensis* (MacFarland 1966), near the middle in *J. mucloc* (Marcus 1958), *J. praeclarus* (Bouchet 1975), *J. toyamensis* (Baba & Abe 1970), and *J. capensis* (present study), or basally in *J. longidentatus* (present study). In most species of *Janolus* all cerata contain extensions of digestive gland except *J. hyalinus* (Eliot 1910), *J. comis* (Marcus 1958), *J. capensis* (present study), and *J. longidentatus* (present study) where the anteriormost cerata are devoid of digestive gland tissue.

It appears that in all species of *Janolus* that have been studied, simple oral glands and elaborate salivary glands are present and the digestive gland occurs as three major branches from the stomach. Anal glands appear to be present in all species except *J. comis* (Marcus 1955) and *J. fuscus* (present study).

TABLE 2
Comparative morphology of *Janolus*.

Species of Janolus	*Colour*	*Ceratal epithelium*	*Ceratal ducts*	*Jaws*	*Radular teeth*
J. australis . .	unknown	smooth ?	unknown	smooth	rachidian and laterals smooth
J. barbarensis . .	translucent white; cerata with gold and blue	smooth	branched	unknown	rachidian smooth, laterals: inner 2 denticulate, outer smooth
J. comis . . .	light brown with dark-brown stipples	papillate	unbranched	smooth	rachidian denticulate, laterals: denticulate, variable
J. cristatus . .	cream or brown with opaque white cerata	smooth	branched at apex	8–12 denticles	rachidian and laterals smooth, rarely denticulate
J. flagellatus . .	unknown	unknown	unknown	smooth	rachidian and laterals smooth
J. fuscus . . .	translucent white with brown lines, cerata with yellow and white	smooth	unbranched	8–14 denticles	rachidian denticulate, laterals: inner 2 denticulate, outer smooth
J. hyalinus . .	cream with red-brown blotches; cerata dotted with white and brown	papillate	unbranched	smooth	rachidian and laterals smooth or finely denticulate
J. indicus . . .	translucent with red-brown spots, cerata grey-green	unknown	unknown	denticulate	rachidian and laterals smooth
J. mirabilis . .	yellow with brown and opaque white; cerata white at apex	papillate	unbranched?	smooth	rachidian, denticulate, laterals: inner 3 denticulate, outer 2 smooth
J. mucloc . . .	transparent white with opaque white lines; cerata with orange spot and opaque white lines	smooth	branched, bifurcate below middle	8 denticles	rachidian denticulate, laterals: inner denticulate, outers smooth
J. novozealandicus	grey with purple stripe and spots; cerata with purple spots	smooth	unbranched	indistinct denticulation	rachidian and laterals smooth
J. praeclarus . .	orange with opaque white; cerata with yellow bands and bluish-white apex	smooth	branched	6 denticles	rachidian and laterals smooth
J. toyamensis . .	yellow with white and brown markings; cerata with yellow spot and red-brown apex	few minute papillae	branched	2 or 3 large denticles	rachidian and laterals smooth
J. capensis . .	translucent white with opaque white; cerata red-brown with opaque white apex	smooth	branched	smooth	rachidian and laterals smooth
J. longidentatus .	translucent white with opaque white; cerata red-brown with opaque white apex	smooth	branched basally	7–8 denticles	rachidian striate, laterals smooth

Radular formula	*Receptaculum seminis*	*Bursa copulatrix*	*Penis*	*Prostatic vas deferens*	*Reproductive ducts*	*References*
24 × 30–54.1.30–54	unknown	unknown	thicker than vas deferens	unknown	unknown	Bergh 1884
16 × 27.1.27	unknown	unknown	unknown	unknown	unknown	Cockerell & Eliot 1905 MacFarland 1966, in part
16 × 12–20.1.12–20 25 × 41.1.41	proximal, serial	absent	conical, flagellar	proximal to penis only	triaulic	Marcus 1955 Marcus 1958
30 × 40.1.40 24 × 33.1.33	proximal, semi-serial	minute, distal	blunt	throughout	diaulic	Alder & Hancock 1851 Alder & Hancock 1855 Schmekel 1970 Thompson & Brown 1976
15 × 20.1.20	unknown	large, elliptical	unknown	unknown	unknown	Eliot 1906
21 × 22.1.22 26 × 25.1.25	proximal, semi-serial	distal	conical	throughout	diaulic	O'Donoghue 1924 MacFarland 1966, in part present study
15 × 11–13.1.11–13	small, proximal, semi-serial	absent	elongate, flagellar	throughout	diaulic	Alder & Hancock 1854*b* Alder & Hancock 1855 Bergh 1888, Eliot 1906, Schmekel 1970
21 × 31.1.31	unknown	unknown	unknown	unknown	unknown	Eliot 1909
20 × 5.1.5	unknown	unknown	unknown	unknown	unknown	Baba & Abe 1970
18 × 24.1.24	proximal, semi-serial within female gland mass	absent	thick	throughout	triaulic	Marcus 1958
23 × 37.1.37	unknown	unknown	short	unknown	unknown	Eliot 1907
20 × 28.1.28	unknown	unknown	unknown	unknown	unknown	Bouchet 1975
20 × 10–20.1.10–20 19 × 25.1.25	proximal	absent	elongate, flagellar	throughout	triaulic	Baba & Abe 1970 present study
20 × 42.1.42 18 × 41.1.41 17 × 26.1.26	elongate, proximal, semi-serial	distal, minute	elongate, flagellar	throughout	diaulic	Bergh 1907 Barnard 1927 present study
18 × 21.1.21 22 × 26.1.26 20 × 20.1.20 21 × 21.1.21	short, proximal, semi-serial	distal, minute	conical	short	diaulic	present study

TABLE 2
Comparative morphology of *Janolus*.

Species of Janolus	*Colour*	*Cerata epithelium*	*Cerata ducts*	*Jaws*	*Radular teeth*
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J. barbarensis . .	translucent white; cerata with gold and blue	smooth	branched	unknown	rachidian smooth, laterals: inner 2 denticulate, outer smooth
J. comis . . .	light brown with dark-brown stipples	papillate	unbranched	smooth	rachidian denticulate, laterals: denticulate, variable
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J. flagellatus . .	unknown	unknown	unknown	smooth	rachidian and laterals smooth
J. fuscus . . .	translucent white with brown lines, cerata with yellow and white	smooth	unbranched	8–14 denticles	rachidian denticulate, laterals: inner 2 denticulate, outer smooth
J. hyalinus . .	cream with red-brown blotches; cerata dotted with white and brown	papillate	unbranched	smooth	rachidian and laterals smooth or finely denticulate
J. indicus . . .	translucent with red-brown spots, cerata grey-green	unknown	unknown	denticulate	rachidian and laterals smooth
J. mirabilis . .	yellow with brown and opaque white; cerata white at apex	papillate	unbranched ?	smooth	rachidian, denticulate, laterals: inner 3 denticulate, outer 2 smooth
J. mucloc . . .	transparent white with opaque white lines; cerata with orange spot and opaque white lines	smooth	branched, bifurcate below middle	8 denticles	rachidian denticulate, laterals: inner denticulate, outers smooth
J. novozealandicus	grey with purple stripe and spots; cerata with purple spots	smooth	unbranched	indistinct denticulation	rachidian and laterals smooth
J. praeclarus . .	orange with opaque white; cerata with yellow bands and bluish-white apex	smooth	branched	6 denticles	rachidian and laterals smooth
J. toyamensis . .	yellow with white and brown markings; cerata with yellow spot and red-brown apex	few minute papillae	branched	2 or 3 large denticles	rachidian and laterals smooth
J. capensis . .	translucent white with opaque white; cerata red-brown with opaque white apex	smooth	branched	smooth	rachidian and laterals smooth
J. longidentatus .	translucent white with opaque white; cerata red-brown with opaque white apex	smooth	branched basally	7–8 denticles	rachidian striate, laterals smooth

Radular formula	*Receptaculum seminis*	*Bursa copulatrix*	*Penis*	*Prostatic vas deferens*	*Reproductive ducts*	*References*
24 × 30–54.1.30–54	unknown	unknown	thicker than vas deferens	unknown	unknown	Bergh 1884
16 × 27.1.27	unknown	unknown	unknown	unknown	unknown	Cockerell & Eliot 1905 MacFarland 1966, in part
16 × 12–20.1.12–20 25 × 41.1.41	proximal, serial	absent	conical, flagellar	proximal to penis only	triaulic	Marcus 1955 Marcus 1958
30 × 40.1.40 24 × 33.1.33	proximal, semi-serial	minute, distal	blunt	throughout	diaulic	Alder & Hancock 1851 Alder & Hancock 1855 Schmekel 1970 Thompson & Brown 1976
15 × 20.1.20	unknown	large, elliptical	unknown	unknown	unknown	Eliot 1906
21 × 22.1.22 26 × 25.1.25	proximal, semi-serial	distal	conical	throughout	diaulic	O'Donoghue 1924 MacFarland 1966, in part present study
15 × 11–13.1.11–13	small, proximal, semi-serial	absent	elongate, flagellar	throughout	diaulic	Alder & Hancock 1854*b* Alder & Hancock 1855 Bergh 1888, Eliot 1906, Schmekel 1970
21 × 31.1.31	unknown	unknown	unknown	unknown	unknown	Eliot 1909
20 × 5.1.5	unknown	unknown	unknown	unknown	unknown	Baba & Abe 1970
18 × 24.1.24	proximal, semi-serial within female gland mass	absent	thick	throughout	triaulic	Marcus 1958
23 × 37.1.37	unknown	unknown	short	unknown	unknown	Eliot 1907
20 × 28.1.28	unknown	unknown	unknown	unknown	unknown	Bouchet 1975
20 × 10–20.1.10–20 19 × 25.1.25	proximal	absent	elongate, flagellar	throughout	triaulic	Baba & Abe 1970 present study
20 × 42.1.42 18 × 41.1.41 17 × 26.1.26	elongate, proximal, semi-serial	distal, minute	elongate, flagellar	throughout	diaulic	Bergh 1907 Barnard 1927 present study
18 × 21.1.21 22 × 26.1.26 20 × 20.1.20 21 × 21.1.21	short, proximal, semi-serial	distal, minute	conical	short	diaulic	present study

As mentioned in the discussion of the synonomy of *Antiopella* with *Janolus* the elaboration of the masticatory border and shape of the jaw are interspecifically variable (Fig. 26). Previous workers (Pruvot-Fol 1954; Marcus 1958) have emphasized the distinctness of a smooth versus denticulate masticatory border. However, *Janolus toyamensis* (Fig. 26C) possesses three large tubercles on the masticatory border and *J. novozealandicus* was described as having indistinct denticles (Eliot 1907).

The radular teeth are variable within *Janolus* (Fig. 27) and some intraspecific variations exists. The rachidian teeth are denticulate in *J. fuscus* (MacFarland 1966; present study), *J. comis* (Marcus 1958), *J. mirabilis* (Baba & Abe 1970), and *J. mucloc* (Marcus 1958), striate in *J. longidentatus* (present study), and smooth in the remaining species. The rachidian tooth has a broad base in species with denticulations or striations and is linear in species with smooth teeth. In *J. fuscus* (MacFarland 1966; present study), *J. mirabilis* (Baba & Abe 1970), and *J. mucloc* (Marcus 1958) the inner 1 to 3 lateral teeth are denticulate while the outer teeth are entirely smooth. *J. cristatus* generally has smooth lateral teeth (Alder & Hancock 1855), but exceptionally (Bergh 1874) they are denticulate. The presence or absence of denticles varies with age in *J. comis* (Marcus 1958) and *J. hyalinus* (Eliot 1906). Bouchet (1975) noted that the lateral teeth of *J. praeclarus* increase in size until the eighteenth row and then begin to diminish. In *J. australis* the innermost are largest (Bergh 1884). In *J. cristatus* (present study) and *J. capensis* (present study) the teeth increase in length on either side of the radula until about one-third of the breadth, and subsequently diminish. In *J. capensis* the radular morphology of fifteen specimens of various sizes did not vary significantly. In *J. hyalinus* (Eliot 1906) and *J. novozealandicus* (Eliot 1907), and in at least ten specimens of *J. longidentatus* (present study) the largest lateral teeth are found at or adjacent to the outer edge of the radula. The relative length of the base to the cusp of the lateral teeth varies considerably between species and appears to be useful in the separation of species.

The central nervous system of *Janolus cristatus* was described (Alder & Hancock 1851) as containing distinct cerebral and pleural ganglia. Bergh noted that these ganglia are fused in *Janolus australis* (Bergh 1884) and *J. capensis* (Bergh 1907). The present study confirms this arrangement in *J. capensis*, while *J. longidentatus* possesses distinct ganglia as in *J. cristatus*.

The morphology of the reproductive system has been fully described in five species of *Janolus*. In *J. comis* and *J. mucloc* (Marcus 1958) the arrangement is triaulic with a short uterine duct connecting the vagina and female gland mass near the separation of the oviduct and vas deferens from the ampulla. In *J. cristatus* and *J. hyalinus* (Schmekel 1970) the vagina joins the female gland mass only at the female atrium, producing an androdiaulic configuration. The present study has shown that *J. toyamensis* (Fig. 28G) has a triaulic arrangement with a proximal receptaculum seminis but with no bursa copulatrix. *J. capensis* and *J. longidentatus* have a diaulic arrangement with a proximal

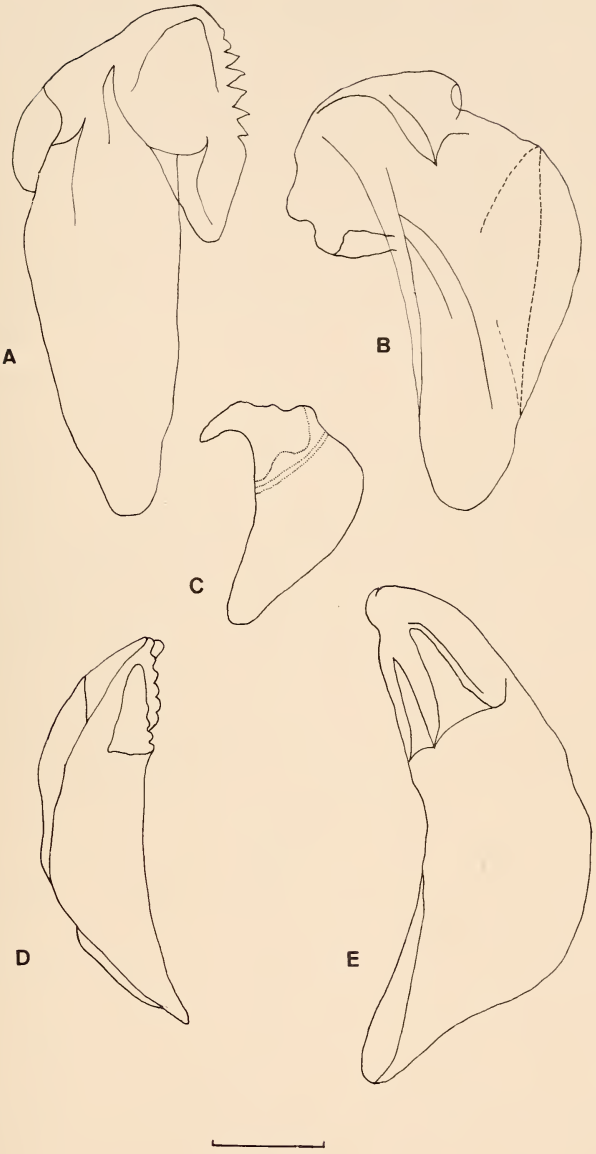

Fig. 26. Variation in jaw morphology. A. *Janolus fuscus* O'Donoghue, 1924. B. *Bonisa nakaza* gen. et sp. nov. C. *Janolus toyamensis* Baba & Abe, 1970. D. *Janolus longidentatus* sp. nov. E. *Janolus capensis* Bergh, 1907. Scale 1,0 mm.

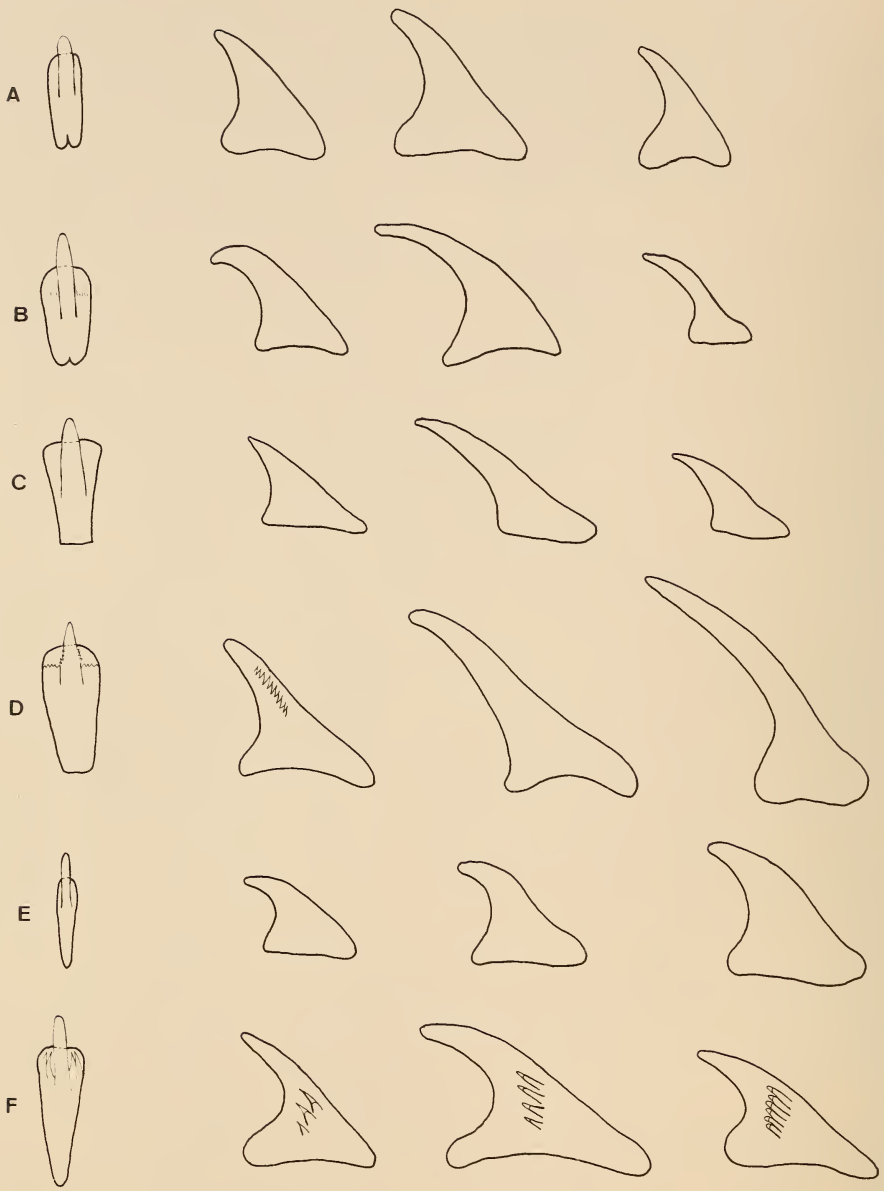

Fig. 27. Variation in the rachidian, first, seventh and twentieth lateral teeth in the Janolidae. A. *Janolus capensis* Bergh, 1907. B. *Janolus longidentatus* sp. nov. C. *Janolus cristatus* (Chiaje, 1841). D. *Janolus fuscus* O'Donoghue, 1924. E. *Janolus toyamensis* Baba & Abe, 1970. F. *Bonisa nakaza* gen. et sp. nov. Not drawn to scale.

receptaculum seminis and a minute, distal bursa copulatrix. This configuration is also present in *J. fuscus* (Fig. 28F) contrary to that described by MacFarland (1966, pl. 64 (fig. 11)).

The shape of the penis has been utilized as a characteristic for specific separation. *Janolus flagellatus* (Eliot 1906) was described as distinct from *J. hyalinus* because its elongate, flagellar penial papilla was thought to be different from the blunt papilla depicted by Bergh (1888) for *J. hyalinus*. Subsequent work by Schmekel (1970) has shown that the penis of *J. hyalinus* is flagellar when fully extended. The shape of the penis varies considerably within species depending on degree of extension. In comparing penial structure between species, it is imperative that descriptions be made from specimens with a fully extended penis.

The egg mass of *Janolus cristatus* (Alder & Hancock, 1855: pl. 44 (figs 6–7)) is a short, convoluted ribbon of about one and a half whorls, with a single egg per capsule. A similar egg mass is apparently present in *Janolus fuscus* (O'Donoghue 1924). The egg mass of *Janolus capensis* (present study) is globose, consisting of many whorls and with 38 to 45 eggs per capsule, while that of *J. longidentatus* is a flat spiral consisting of 5–9 eggs per capsule.

Janolus longidentatus differs from all other species of *Janolus* which possess denticles on the masticatory edge. *J. mucloc* (Marcus 1958) is triaulic and therefore differs from the diaulic *J. longidentatus*. *J. praeclarus* (Bouchet 1975), while much of its anatomy remains unknown, differs from *J. longidentatus* in its orange versus translucent white coloration, smaller inter-rhinophoral crest, branching of the ceratal ducts near the middle rather than basally, more sharply arched radular teeth that are longest near the middle rather than at the outer edge of the radula, and jaws with 6 denticles rather than 7 or 8. *Janolus longidentatus* differs from *J. fuscus* in its coloration, more elaborate inter-rhinophoral crest, smooth inner lateral teeth, and presence of anal glands. *Janolus longidentatus*, although similar to *J. cristatus* in coloration, external and reproductive anatomy (Schmekel 1970), differs in several significant aspects. In *J. longidentatus* the ceratal ducts branch basally while they branch apically in *J. cristatus*. The rachidian teeth of *J. longidentatus* are broad with striations versus the smoothly linear form of *J. cristatus*. In *J. cristatus* the radular teeth are largest at the inner third of the radula, while they are broadest near the outer margin in *J. longidentatus*. The lateral teeth are broader and heavier in *J. cristatus*. The oviduct is short in *J. cristatus* and elongate in *J. longidentatus*. *J. cristatus* has a blunt club-shaped penis, while in *J. longidentatus* it is conical.

Despite the difference in the elaboration of the masticatory border of the jaw, *J. longidentatus* most closely approaches *J. capensis* in its morphology. For this reason a morphological comparison of the three sympatric South African janolids is provided in Table 3.

The South African species of janolids occur together in the shallow waters of False Bay. All three species can be found within a few centimetres of each other. *Janolus capensis* and *J. longidentatus* have been observed to feed upon

TABLE 3
Comparative morphology of South African janolids.

	Bonisa nakaza	*Janolus capensis*	*Janolus longidentatus*
body	stout	stout	slender
inter-rhinophoral crest	low, few convolutions	high, many convolutions	high, many convolutions
ceratal ducts	absent	multifid, irregular, near middle	quadrifid, regular, near base
gonopore	near middle of body	near middle of body	anterior third of body
nephroproct	posterior third of body	posterior to middle of body	near middle of body
mouth opening	oblong	oblong	round
salivary glands	with basal reservoir	taper at insertion	glandular at insertion
masticatory border	smooth	smooth	7–8 denticles
rachidian tooth	broad, with large denticles	smooth, linear	broad, with striations
largest laterals	innermost teeth	third of width of radula	near outer margin of radula
lateral teeth	hook-shaped, denticulate	hook-shaped, smooth	with elongate cusp, smooth
cerebral and pleural ganglia	distinct	fused	distinct
penis	club-shaped, corrugated	flagellar	conical
vas deferens	short, straight	highly convoluted	with few convolutions
receptaculum seminis	large, saccate	elongate, as long as vagina	short, quarter of vaginal length
eggs/capsule	1 or 2	38–45	5–9

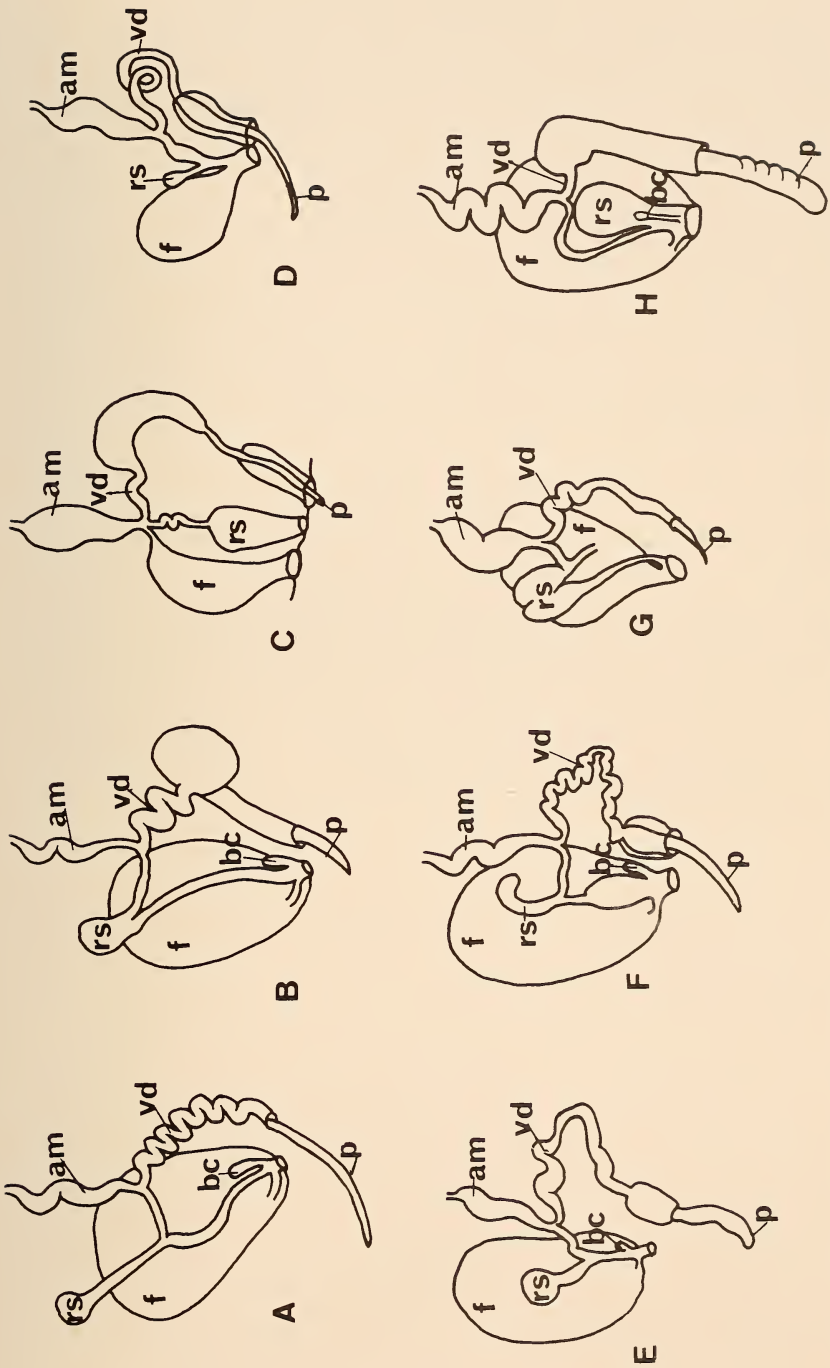

Fig. 28. Variation of reproductive system in *Janolus*. A. *Janolus capensis* Bergh, 1907 (present study). B. *Janolus longidentatus* sp. nov. (present study). C. *Janolus comis* Marcus, 1955 (after Schmekel 1970). D. *Janolus hyalinus* (Alder & Hancock, 1854) (after Schmekel 1970). E. *Janolus cristatus* (Chiaje, 1841) (after Schmekel 1970). F. *Janolus fuscus* O'Donoghue, 1924 (present study). G. *Janolus toyamensis* Baba & Abe, 1970 (present study). H. *Bonisa nakaza* gen. et sp. nov. (present study). Not drawn to scale.

the same species of ectoproct, while *Bonisa nakaza* feeds on a more heavily calcified species. Food abundance does not appear to be a limiting factor as many ectoproct colonies are devoid of janolids. Observation of feeding behaviour in *Janolus capensis* and *J. longidentatus* has produced no apparent differences in mode of feeding or handling of prey. No obvious form of resource partitioning has been observed between the two species, although it may exist.

The hottentot, *Pachymetopon blochii*, is the most common fish species in environments where janolids have been observed and is known to be a generalized omnivore of benthic organisms (Nepgen 1977). Specimens of *Bonisa nakaza*, *Janolus capensis*, and *J. longidentatus* are readily ingested by hottentots in the field and even more readily regurgitated in an unharmed state, suggesting defensive immunity to fish predation. More detailed study of the three species of janolids is required to determine their competitive population dynamics, interaction, and possible resource partitioning.

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